



Review article

Revisiting the possibility of reciprocal help in non-human primates

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ARTICLE INFO

Keywords:

Evolution
Cooperation
Reciprocity
Exchange
Help
Market
Primates

ABSTRACT

Reciprocity is a ubiquitous and important human trait. Still, the evolutionary origin is largely unclear, partly because it is believed that our closest living relatives, other primates, do not reciprocate help. Consequently, reciprocity is suggested to have evolved in the human lineage only. However, our systematic review of studies investigating reciprocity in non-human primates revealed that, contrary to common perception, there are more positive than negative findings in both experimental and observational studies. Furthermore, we argue that negative findings can provide important insights. We found that reciprocity is not confined to unrelated individuals. In addition, reciprocity can be influenced by the choice of experimental design, relationship quality, social services and temporal scales. Thus, negative findings should not be used as evidence of no reciprocity but as the building blocks for a more comprehensive theory. Based on our review, we conclude that reciprocity in primates is present but underestimated. We close by suggesting further steps that could pave the way for future research aimed at understanding the evolutionary origins of reciprocity.

1. Introduction

Many animals cooperate by helping each other, i.e. providing benefits to others, which is one type of prosocial behaviour (Jensen, 2016). Such help is multifarious and ubiquitous in nature. Help can range from sacrificing one's own life to facilitate others reproduction, e.g. social amoeba (*Dictyostelium discoideum*, Strassmann and Queller, 2011) to foregoing reproduction to raise the offspring of others, e.g. eusocial insects (Wilson and Hölldobler, 2005). Helping others to breed more efficiently is widespread and shown, for instance, in fish that defend and care for others' offspring (*Neolamprologus pulcher*, Taborsky, 2016). Furthermore, helping is not restricted to breeding contexts, as many birds preen each other's feathers (e.g. *Cantorchilus leucotis*, Gill, 2012) and some monkeys provide food to each other (e.g. *Cebus apella*, de Waal, 1997b). In addition, humans help others in a variety of circumstances and even help strangers, for instance, by donating blood (Lacetera and Macis, 2010).

Despite its prevalence, helping appears to be detrimental at first sight, as it benefits somebody else on own costs (Darwin, 1859). Hence, the evolution of helping has been controversially discussed for decades and remains a prevailing topic (Pennisi, 2005). Gaining indirect fitness benefits by helping relatives is often used as an explanation for cooperative interactions (Hamilton, 1964). However, such nepotism cannot exclusively explain the evolution of helping, as help is not limited to related partners (Dugatkin, 2002). One possibility for the

evolution of helping between non-kin is reciprocity (Trivers, 1971). Here, helping is conditional on a partner's cooperativeness and is often illustrated by the rule "I help you because you helped me" (Trivers, 1971). By exchanging favours repeatedly, partners engaged in reciprocity are better off than those that never help others and consequently never receive any benefits in return (Axelrod and Hamilton, 1981).

Reciprocity is omnipresent in the daily life of humans (reviewed in Bowles and Gintis, 2011). Reciprocity is evident in direct interactions between familiar partners like relatives, friends and partners (Allen-Arave et al., 2008; Buunk and Schaufeli, 1999) and unfamiliar partners (Andreoni and Miller, 1993). Even in the absence of potential returns, humans help others by, for instance, anonymously donating blood (Lacetera and Macis, 2010), which can be explained by indirect reciprocity (Boyd and Richerson, 1989). That is by helping others, people increase their reputation, which will increase the possibility to receive help themselves by bystanders. Such a good reputation can translate into direct benefits because humans are more likely to help such cooperating partners, even if they have never directly interacted with them before (Wedekind and Milinski, 2000). Furthermore, humans use not only information about the cooperativeness of partners but use also information about whether a defector intentionally withdrew from helping others. Here, observers are even willing to pay money to punish such defecting partners (Fehr et al., 2002). But reciprocity does not only play a role during day-to-day interactions between single individuals. It

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Received 23 February 2019; Received in revised form 12 June 2019; Accepted 20 June 2019

Available online 28 June 2019

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also occurs on a much larger scale, e.g. between interacting nations (Frank et al., 2018). Finally, reciprocity has resulted in major changes in human societies on an evolutionary time scale, because reciprocity enabled the division of labour, e.g. parental care traded for food provision, from which hunter-gatherer societies have emerged (Durkheim, 1984). Given this importance on different scales, the term *Homo reciprocans* has been proposed to illustrate the importance of reciprocity in human cooperation (Bowles et al., 1997).

The term *Homo reciprocans* suggests reciprocity being a uniquely human trait. Indeed, some researchers conclude that reciprocity is rare in other animals (e.g. Clements and Stephens, 1995; Clutton-Brock, 2009; Connor, 2010; Hammerstein, 2003; Hauser et al., 2009; Stevens et al., 2005; West et al., 2007). This view is based on several arguments. First, it has been suggested that cooperation between unrelated individuals is rare and hence there is no need for a mechanism to evolve to ensure cooperation between non-kin (Clutton-Brock, 2009). Second, there is a perceived absence of evidence for reciprocity, leading to the conclusion that it is a rare phenomenon (Hammerstein, 2003). Finally, it has been proposed that reciprocity is rare because it is cognitively too complex for animals other than humans (Hauser et al., 2009; Ramseyer et al., 2006; Russell and Wright, 2009; Sánchez-Amaro and Amici, 2015; Stevens et al., 2005; Stevens and Gilby, 2004; Stevens and Hauser, 2004, 2005).

This stands in sharp contrast to other researchers who conclude that reciprocity is widespread in non-human animals (e.g. Carter, 2014; Schino and Aureli, 2010b; Silk, 2013; Taborsky et al., 2016). Already 25 years ago, Taborsky (1994) summarised evidence for 33 fishes that potentially exchange favours reciprocally. Díaz-Muñoz and co-workers (2014) listed 87 species, ranging from spiders to mammals, that show reciprocity in the context of reproduction. In a recent review, Taborsky and colleagues (2016) collected evidence for over 160 species that exchange any kind of help reciprocally from allopreening to defence and vigilance. These reviews consider both observational and experimental evidence and the authors indicated that probably more species than those listed are capable of reciprocity. In addition, complex calculations might not be needed for reciprocity, i.e. calculated reciprocity, because there are also cognitively less demanding mechanisms that can underlie reciprocity, such as hard-wired, attitudinal or emotion-based reciprocity (Brosnan and de Waal, 2002; Schino and Aureli, 2009; Schweinfurth and Call, 2019).

We think this controversial debate can be enriched by investigating evidence for reciprocal cooperation in non-human primates, a taxon that has been extensively studied in terms of cooperation. In addition, as humans are primates, it seems obvious to search for reciprocity in our closest living relatives in order to understand the evolutionary origins of (human) reciprocity. However, non-human primates have been suggested to show a lack of reciprocity for the reasons mentioned earlier. By reviewing evidence for reciprocity in extant non-human primates, we aim at investigating the evolutionary roots of reciprocity. First, we will review the evidence for reciprocity in non-human primates in observational (OS) and experimental studies (ES), which complement each other (see the supplementary material for our categorisation criteria). While there is a large body of positive findings, there are also some negative findings in both OS and ES. We will highlight potential reasons for negative findings and what can be learned from them. We will close our review by evaluating the existence of reciprocity in non-human primates, which will inform the evolution of (human) reciprocity.

2. Meeting the preconditions of reciprocity

We begin our review by considering a basic question: how likely reciprocity is to evolve in non-human primates. When Trivers (1971) proposed the theory of reciprocity, he named several social-life parameters that would favour its evolution: long lifetime to increase interactions, low dispersal to increase encounters, mutual dependence to

increase sociality, parental care to increase dependence, flat hierarchy to reduce asymmetry and agonistic support to increase need for allies. Later, Dugatkin (2002) added two fundamental cognitive processes that are inevitably required for reciprocity: individual recognition and memory of previous encounters.

Here, we will review whether primates fulfil the preconditions of reciprocity and whether it is expected to evolve in primates. The primate order is a large phylogenetic group with at least 261 species (Perelman et al., 2011) with great diversity in social systems, from strictly solitary to highly social species (Kappeler, 1997). Such remarkable diversity makes general statements difficult, which is why we will restrict our discussion to basic patterns. However, the social-life parameters, pointed out by Trivers, seem to characterise the social life of most of primates. First, primates are among the longest-lived animals on earth (Austad and Fischer, 1992). Second, in most primate groups dispersal is somehow limited, leading to stable groups. Despite a high diversity in group structure, the vast majority of species live in stable mixed-sex groups containing three or more adults (Kappeler and van Schaik, 2002). Third, mutual dependence is shown by close social bonds in which individuals frequently exchange affiliative behaviours like allogrooming, alloparenting, combat aid, food sharing and other more species-specific helpful behaviours (reviewed for example in: Silk, 2007a). Such mutually dependent relationships have important life-long effects, e.g. offspring of baboon mothers with strong social bonds live longer (Silk et al., 2009). Fourth, like most mammals, primate mothers heavily invest in the care of their offspring by, for example, lactating. Fifth, a number of species show shallow dominance hierarchies, although many others show pronounced hierarchies (Eisenberg et al., 1972), which is why it cannot be assumed that primates generally show flat hierarchies. Finally, many primates form alliances to out-compete other group members (Harcourt, 1988).

With regard to cognitive preconditions, most primates appear to possess the cognitive processes required for reciprocity. First, there is good evidence that most primates individually recognise conspecifics, generally using acoustic (e.g. Townsend et al., 2012) and visual cues (Ghazanfar and Santos, 2004). The second prerequisite, memory of previous encounters, is more difficult to test as it is comprised of multiple skills. Throughout the order of primates, however, they show sophisticated social memory skills, such as 3rd party knowledge, long-term memory of individuals and events (Beran, 2004; Janson, 2016; Keenan et al., 2016; Lewis et al., 2017; Martin-Ordas et al., 2013; Matthews and Snowdon, 2011; Tomasello and Call, 1997, 1994). This suggests that memorising previous encounters with specific individuals, underlying reciprocity, is within the cognitive skillset of most primates.

Hence, their social life parameters seem to favour the evolution of reciprocity. Furthermore, most primate species seem to fulfil the basic cognitive preconditions to reciprocate help. Ever since Trivers proposed the theory of reciprocity, several OS and ES have been conducted to test whether primates indeed reciprocate. Based on these studies, the role of reciprocity in non-human primate cooperation has been questioned (cf. Cheney, 2011; Clements and Stephens, 1995; Clutton-Brock, 2009; Hammerstein, 2003; McAuliffe and Thornton, 2015; Ramseyer et al., 2006; Schino and Aureli, 2009; Silk, 2013; Stevens et al., 2005; Stevens and Gilby, 2004; Taborsky et al., 2016). Nevertheless, before drawing conclusions about the importance of reciprocity in non-human primates, we propose to go one step back and scrutinise the existing literature.

3. The evidence of reciprocity: observational studies

We identified more than 130 OS testing reciprocity in over 40 primate species by a systematic literature search, using google scholar, ISI web of knowledge and PrimateLit. Due to space limitations, we provide a full list of the OS in the supplementary material (please see also the supplementary material for our search and inclusion criteria). Of these studies, more tests found evidence for than against reciprocity (> 80%,

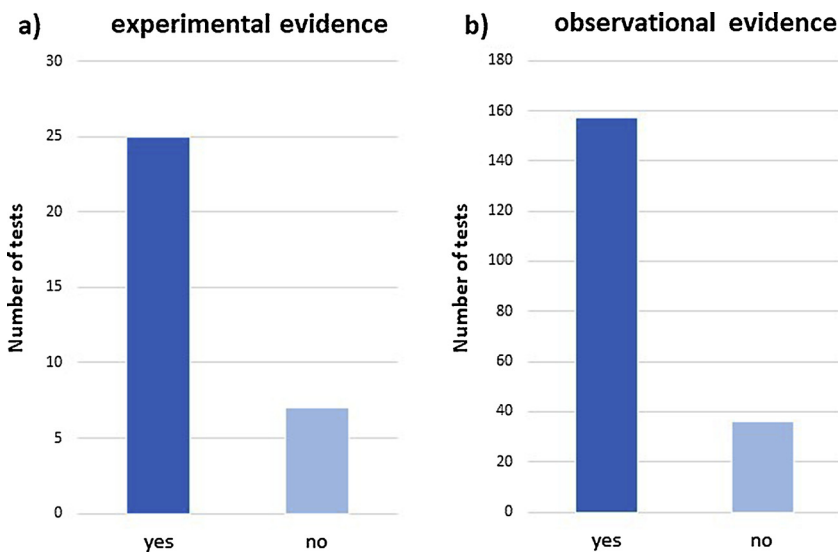


Fig. 1. Evidence of reciprocity in primates.

We identified more than 130 OS (panel a) investigating reciprocity in 41 non-human primate species and 31 ES (panel b) investigating reciprocity in 11 primate species. For those studies reporting data on multiple species or commodities, we considered each test as a separate data point in our analysis (OS: $n = 193$, tab. S1, ES: $n = 40$, Table 1). We restricted our analysis to tests whose outcomes were unambiguous and could not be explained by a lack of motivation or task understanding mentioned by the authors in their articles ($n = 32$). Tests of both study types reported more positive than negative findings.

Fig. 1, tab. S1). Our result is consistent with meta-analyses, which provide a more systematic overview of subsets of the data and which correct for publication bias. They show that allogrooming is reciprocally exchanged for agonistic support (Schino, 2007), food (Jaeggi and Gurven, 2013a) and allogrooming (Hemelrijk and Luteijn, 1998; Schino and Aureli, 2010b, 2008). Additionally, non-human primates reciprocate food for food (Jaeggi and Gurven, 2013a).

The evidence for reciprocity is diverse, including different behaviours, contexts, environments and species. To illustrate these results in more detail, we describe evidence for reciprocity in chimpanzees (*Pan troglodytes*); the species that has received the most research attention. Studies on captive individuals have demonstrated the reciprocal exchange of allogrooming (Hemelrijk and Ek, 1991), support (de Waal and Luttrell, 1988), consolation (Romero et al., 2010) and food (Jaeggi and Gurven, 2013a). Moreover, reciprocity can take place between different commodities. Hence, captive chimpanzees have been shown to exchange food for allogrooming (de Waal, 1997b) and allogrooming for sex (Hemelrijk et al., 1992). Similarly under natural conditions, chimpanzees reciprocate allogrooming for allogrooming (Newton-Fisher and Lee, 2011; Nishida, 1988), allogrooming for meat (Mitani, 2006), allogrooming for support (Watts, 2002), meat for meat (Mitani and Watts, 1999), meat for sex (Gomes and Boesch, 2009) and meat for support (Mitani, 2006). Furthermore, probably even more than two commodities may be reciprocated as studies on captive (de Waal, 1982) and wild chimpanzees suggest (Gomes and Boesch, 2011; Goodall, 1986). Finally, there is evidence for reciprocity derived by partner control, indicated by correlations between received and given favours within dyads (de Waal, 1997b; Gomes and Boesch, 2011), as well as partners choice, indicated by correlations between social bonds and exchanged behaviours (Jaeggi et al., 2013; Samuni et al., 2018; reviewed in Schino and Aureli, 2017). Taken together, these studies present a strong case that given and received help of various kind are correlated between individuals, suggesting reciprocity being of great importance.

Although there is good evidence for reciprocity in various primate species, it should be noted that approximately 20% of all correlations between given and received help did not provide evidence of reciprocity (reviewed in: Sánchez-Amaro and Amici, 2015). On the one hand, a lack of correlation might indicate that reciprocity may not be exhibited under some circumstances. On the other hand, a recent study illustrates how easily correlations can be masked by other factors, even though they are present (Carter et al., 2019). Most primates live together with related and unrelated individuals and nepotism is widespread (Silk, 2002a). Yet, nepotism can mask reciprocity, mainly because nepotism is easier to estimate than reciprocal relationships that

may change over time or take place between commodities or over long periods. This effect is especially apparent when tests are based on small sample sizes (Carter et al., 2019). As a result, non-significant results of reciprocity should be treated with caution and the possibility of reciprocity should not be rejected prematurely in such studies.

Taken together, over 80% of the tests provide evidence that given and received goods and services are correlated in primates, making reciprocity a likely explanation for cooperation. This large body of findings is highly interesting as the studies demonstrate the occurrence of a natural behaviour under relevant natural conditions. However, while OS provide a strong case in favour of reciprocity, correlations are not suited to provide a causal relationship between exchanged favours due to potential third variables (Milinski, 1997; Seyfarth and Cheney, 1988; Silk, 2007b). Possible confounding variables that may lead to correlations between given and received favours are, for instance, spatial proximity (Puga-Gonzalez et al., 2015), hierarchical symmetry (Hemelrijk and Ek, 1991) or kin relationships (Curtis et al., 2003). Even though some OS have statistically controlled for such variables, studies can only assess whether provided help is causally contingent on experienced help by manipulating received helping to exclude by-products of other variables.

4. The evidence of reciprocity: experimental studies

In contrast to OS, the amount of ES is surprisingly small ($n = 31$) and limited to 11 primate species. Here, we provide an overview of all published ES, as far as we know, on reciprocity in non-human primates (Table 1).

The best-known experimental example for reciprocity is probably the capuchin monkey (*Cebus apella*). Capuchins have been repeatedly shown to exchange food reciprocally using various methods. They handed over food to a partner housed in a separate compartment (de Waal, 2000, 1997a), pulled a baited platform within reach of a partner (de Waal and Berger, 2000; Mendres and de Waal, 2000), or pulled levers of a box that benefited a partner (Leimgruber et al., 2014). Even in more abstract tasks, i.e. dividing sequential actions, manoeuvring digital joysticks or exchanging valuable tokens, capuchins provided food to a partner reciprocally (Hattori et al., 2005; Parrish et al., 2015; Suchak and de Waal, 2012). In such exchanges, capuchins not only considered donation rates but also the quality of their and their partner's food (de Waal, 2000). In contrast to these experiments, capuchins did not reciprocate food when pulling a baited platform (Amici et al., 2014) or exchanging valuable tokens (Pelé et al., 2010). Both results might be explained by a lack of task understanding as pointed out by

Table 1
Overview of experimental evidence on reciprocal helping in non-human primates. This table summarises 40 experimental tests investigating reciprocity in 11 primate species, reported in 31 studies.

Species	Commodity	Task	Mechanism	Dyad	N	Benefits	Reciprocity	Location	Reference
Bonobos (<i>Pan paniscus</i>)	food	bar pulling token exchange	partner control partner control	adult & juvenile –	5 5	partner actor vs. actor & partner	N ¹ N ¹	Wolfgang Koehler Primate Research Center, Leipzig Zoo (Germany)	(Amici et al., 2014) (Pelé et al., 2009)
Capuchin monkeys (<i>Cebus apella</i>)	food	bar pulling	partner control	–	7	partner	N ¹	Istituto di Scienze e Tecnologie della Cognizione, Unit of Cognitive Primatology & Primate Center in Rome (Italy)	(Amici et al., 2014)
			partner control	unrelated, same sex	14	partner	Y	Yerkes National Primate Research Center, Emory University (USA)	(de Waal and Berger, 2000)
		computer task	partner control	unrelated, same sex	10	partner	Y	Language Research Center, Georgia State University (USA)	(Mendres and de Waal, 2000)
		pulling a lever out of a box	partner control	–	10	partner	Y	Graduate School of Letters, Kyoto University (Japan)	(Parrish et al., 2015)
			partner control	unrelated, 1 juvenile	6	partner	Y ¹	University (Japan)	(Hattori et al., 2005)
			partner control	–	4	actor & partner	Y ¹	Comparative Cognition Laboratory, Yale University (USA)	(Leimgruber et al., 2014)
		spontaneous sharing	partner control partner control partner choice vs. partner control	mostly unrelated mostly unrelated related	13 13 11	partner partner partner	Y Y Y ¹	Yerkes National Primate Research Center, Emory University (USA)	(de Waal, 2000)
								Istituto di Scienze e Tecnologie della Cognizione, Unit of Cognitive Primatology & Primate Center in Rome (Italy)	(de Waal, 1997a) (Sabbatini et al., 2012)
Chacma baboons (<i>Papio hamadryas ursinus</i>)	attention for grooming	playback	partner choice	related & unrelated, ♀, juvenile & adult, wild born	23	–	Y (in non-kin)	Primate Research Institute, University of Strasbourg (France)	(Pelé et al., 2010)
		token exchange	partner control	–	4	partner or actor & partner	N ¹	Yerkes National Primate Research Center, Emory University (USA)	(Suchak and de Waal, 2012)
		button box	partner control	unrelated, familiar & unfamiliar	12	partner or actor & partner	Y	Moremi Game Reserve (Botswana)	(Cheney et al., 2010)
Chimpanzees (<i>Pan troglodytes</i>)	food	bar pulling	partner control	adult & juvenile	9	partner or actor & partner	N ¹	Primate Research Institute, Kyoto University (Japan)	(Yamamoto and Tanaka, 2010)
		loose-string	partner control	–	13	actor or actor & partner	N	Wolfgang Koehler Primate Research Center, Leipzig Zoo (Germany)	(Amici et al., 2014)
		token exchange	partner control	unrelated, adult & juvenile, wild born adult & juvenile	12 12 4	partner partner or actor & partner	Y (in 2/6 pairs) ¹ N ¹ N ¹	Keeling Center for Comparative Medicine and Research, University of Texas (USA) Ngamba Island Chimpanzee Sanctuary (Uganda)	(Brosnan et al., 2009)
		trust game	partner control	unrelated	15	actor vs. actor & partner	Y	Wolfgang Koehler Primate Research Center, Leipzig Zoo (Germany)	(Melis et al., 2009)
		vending machine	partner control	unrelated, wild & captive born	6,12	partner or actor or actor & partner	Y	Sweetwaters Chimpanzee Sanctuary (Kenya)	(Melis et al., 2016) (Pelé et al., 2009)
		bar pulling	partner control	–	8	actor or actor & partner	Y	Wolfgang Koehler Primate Research Center, Leipzig Zoo (Germany)	(Engelmann et al., 2015)
		recruitment	partner choice	unrelated, adult & juvenile, wild born unrelated, adult & juvenile, wild born	10	actor or actor & partner	Y	Prime Research Institute, Kyoto University (Japan)	(Engelmann and Herrmann, 2016)
			partner choice					Wolfgang Koehler Primate Research Center, Leipzig Zoo (Germany)	(Yamamoto and Tanaka, 2009)
								Ngamba Island Chimpanzee Sanctuary (Uganda)	(Schmelz et al., 2017)
									(Melis et al., 2006a)
									(Melis et al., 2008)

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Table 1 (continued)

Species	Commodity	Task	Mechanism	Dyad	N	Benefits	Reciprocity	Location	Reference
Cotton-top tamarins (<i>Saguinus oedipus</i>)	food	bar pulling	partner control	mixed sex	12, 14	partner or actor & partner	Y	Psychology Department, University of Wisconsin (USA)	(Cronin et al., 2010)
			partner control	unrelated	5-7	actor or partner or actor & partner	Y	Primate Cognitive Neuroscience Lab, Harvard University (USA)	(Hauser et al., 2003)
Gorillas (<i>Gorilla gorilla</i>)	food	bar pulling	partner control	adult & juvenile, wild & captive born	4	partner	N [*]	Wolfgang Kohler Primate Research Center, Leipzig Zoo	(Amici et al., 2014)
		token exchange	partner control	Q	3	actor vs. actor & partner	N ¹		(Pelé et al., 2009)
Long-tailed macaques (<i>Macaca fascicularis</i>)	support for grooming	application of syrup	partner choice	Unrelated, Q	?	partner	Y	Field station Bockengut, University of Zurich (Switzerland)	(Hemelrijk, 1994)
Orang-utans (<i>Pongo pygmaeus</i>)	food	bar pulling	partner control	adult & juvenile	4	partner	Y (in 1 pair)	Wolfgang Kohler Primate Research Center, Leipzig Zoo (Germany)	(Amici et al., 2014)
		token exchange	partner control	–	2	actor vs. actor & partner	Y (in 1 pair) ¹		(Dufour et al., 2009)
			partner control	–	5	actor vs. actor & partner	Y (in 1 pair) ¹		(Pelé et al., 2009)
Spider monkeys (<i>Ateles geoffroyi</i>)	food	bar pulling	partner control	adult & juvenile, wild born	7	partner	N [*]	Animaya Zoo (Mexico)	(Amici et al., 2014)
Tonkesean macaques (<i>Macaca tonkeana</i>)	food	token exchange	partner control	–	3	partner or actor & partner	N [*]	Primate Centre, University of Strasbourg (France)	(Pelé et al., 2010)
Vervet monkeys (<i>Chlorocebus aethiops</i>)	attention for grooming	playback	partner choice	related & unrelated, Q, juvenile & adult, wild born	11,?	–	Y (in non-kin)	Amboseli National Park (Kenya)	(Seyfarth and Cheney, 1984)
	grooming for food	selective food provisioning	partner choice	related & unrelated, juvenile & adult, wild born	?	partner & actor [#]	Y	Loskop Dam Nature Reserve (South Africa)	(Fruteau et al., 2009)
	grooming for tolerance		partner choice	related & unrelated, Q, wild born	12	actor & partner	Y	Mawana Game Reserve (South Africa)	(Borgeaud and Bshary, 2015)
			partner choice	related & unrelated, Q, wild born	17	actor & partner	Y		(Borgeaud et al., 2017)

Unless otherwise stated, the dyads consisted of captive-born adult (> 8 years) individuals of both sex that were familiar to each other.

¹ No task-understanding control has been reported or referred to in the respective studies.

* It is unclear whether test subjects understood the task as their response did not differ between their partner being absent or present.

It is an ongoing debate whether grooming is mainly beneficial for groomees or for both groomers and groomees (see [Dunbar, 1991](#)).

the authors. A clever experiment presented capuchin monkeys with two instead of one partner to test for the mechanism underlying their reciprocity. Here, direct food transfers were rather based on positive relationship scores than on received food, suggesting long-term exchanges are of greater importance than short-term exchanges (Sabbatini et al., 2012).

While the overall evidence in capuchins is convincing, results from ES on chimpanzees, are far more mixed. For instance, chimpanzees were tested in a task in which a baited platform could be pulled within a partner's reach (Amici et al., 2014). Although chimpanzees provided more food to a partner that could retrieve the rewards, overall their pulling rate did not match the number of received donations. Some evidence for mirroring donations rates was, however, obtained in the loose-string task (Melis et al., 2009). Here, two individuals needed to pull a string simultaneously to bring a mutually rewarding platform into their reach. When the platform was baited with food of different value, two out of six pairs provided almost equal amounts of food in a series of trials. This suggests some form of reciprocity at least in these two pairs. This possibility was further corroborated by a study in which test subjects could decide to pull a no-trust rope, resulting in a low value selfish reward, or a trust-rope, resulting in high value food upon their partner's decision. Chimpanzees were more likely to trust a socially bonded individual (Engelmann and Herrmann, 2016). In this study, social bonds were characterised by affiliative behaviours over a long-time scale. Hence, trusting a socially bonded partner might be the result of long-term reciprocity. Furthermore, the authors showed in another study, using the same task, that chimpanzees trusted some partners more than others to engage in reciprocity (Engelmann et al., 2015). Direct evidence for reciprocity in chimpanzees comes from a loose-string task, in which test subjects helped a partner more often to gain food that previously helped them (Melis et al., 2008). In the same task, chimpanzees chose to cooperate with the best collaborator, suggesting partner choice based on previous help and thus reciprocity (Melis et al., 2006a). In contrast, chimpanzees did not take turns during cooperative interactions: they neither exchanged roles in exchanging tokens among them (Pelé et al., 2009), nor in inserting tokens into a vending machine (Yamamoto and Tanaka, 2009) or in pulling ropes in the loose-string task (Melis et al., 2016) to reach equal rewards for their partner and themselves. Another line of research investigated whether individuals choose to provide benefits only to themselves or to themselves and a partner at no extra cost, i.e. prosocial choice task. In such a task, chimpanzees were not more likely to choose a platform that resulted in food for both, when this partner had provided food to them before (Brosnan et al., 2009; Silk et al., 2005). This stands in contrast to a recent study, in which chimpanzees were more likely to choose the prosocial and even altruistic option over a selfish option after their partner had assisted them, suggesting reciprocity to be a motivator of prosocial actions (Schmelz et al., 2017; for comments see: Brosnan, 2017).

Reciprocity has been tested repeatedly in vervet monkeys (*Chlorocebus aethiops*). Early work showed that these monkeys were more likely to attend to playbacks of support solicitation calls, after they had been groomed by this partner (Seyfarth and Cheney, 1984). It is important to note that the authors did not manipulate received allogrooming, but rather used naturally occurring allogrooming events and manipulated the need to receive help by playing solicitation calls. Thereby, they demonstrated short-term reciprocity. However, without manipulating received allogrooming, it is currently unclear whether other factors, such as proximity instead of allogrooming, may explain the increased attention to the playback. More recently, an elegant experiment on free-ranging individuals showed an increase in allogrooming effort towards artificially created food providers compared to non-providers (Borgeaud et al., 2017; Fruteau et al., 2009). Their probability to reciprocate was further highlighted by exchanges with different commodities, such as social tolerance being reciprocated with allogrooming (Borgeaud and Bshary, 2015).

Besides these three rather well-investigated species, there have been only few studies on other primate species. Within apes, only orangutans (*Pongo pygmaeus*) have been repeatedly shown to reciprocate tokens that delivered food only to their partner (Amici et al., 2014; Dufour et al., 2009; Pelé et al., 2009). It should be noted, however, that this evidence is based mainly on one dyad (Bimbo and Dokana) that reliably reciprocated tokens, leading to results that are not independent from each other. Although bonobos (*Pan paniscus*) were shown to cooperate over multiple sessions at high levels (Hare et al., 2007), they seem to show no signs of reciprocity (Amici et al., 2014; Pelé et al., 2009). Similarly, gorillas (*Gorilla gorilla*) did not show any evidence of reciprocity when pulling a baited platform into reach of a partner (Amici et al., 2014) or when exchanging valuable tokens with each other (Pelé et al., 2009). It should be noted, however, that neither bonobos nor gorillas passed the task-understanding control, which was benefitting a partner over an empty compartment (Amici et al., 2014; Pelé et al., 2009).

Lastly, there are only a few studies investigating reciprocity in monkeys other than vervet or capuchin monkeys. Long-tailed macaques (*Macaca fascicularis*), which experienced experimentally induced enhanced allogrooming levels by a partner, reciprocated afterwards by providing agonistic support (Hemelrijk, 1994). In contrast, closely related Tonkean macaques (*Macaca tonkeana*) did not engage in reciprocity in a token exchange task, although this could be again a result of limited task understanding (Pelé et al., 2010). In a similar playback experiment described earlier for vervet monkeys, chacma baboons (*Papio hamadryas ursinus*) directed their attention to a partner that had groomed them but not to another that had aggressed them (Cheney et al., 2010). This shows that attention was contingent on recent socio-positive but not on socio-negative experiences. Likewise, cotton-top tamarins (*Saguinus oedipus*) increased their food donations to a partner via a baited platform, but only if there was a possibility to reciprocate (Cronin et al., 2010; Hauser et al., 2003). Finally, spider monkeys (*Ateles geoffroyi*) did not show any evidence of reciprocity when pulling a baited platform within reach of a partner, whereas it was unclear whether they understood the task, as they did not provide more food to a partner that could reach the food compared to a partner that could not reach the food (Amici et al., 2014).

Taken together, experimental evidence for reciprocity among primates seems to be mixed. Results vary across and within species and methodologies (Table 1). The perceived absence of consistent evidence for reciprocity in well-controlled experiments has led to the belief that reciprocity is rare or absent in primates other than humans and thus to the rejection of reciprocity as an underlying mechanism of cooperation in primates other than humans (e.g. Clements and Stephens, 1995; Clutton-Brock, 2009; Hammerstein, 2003; McAuliffe and Thornton, 2015; Ramseyer et al., 2006; Stevens et al., 2005; Stevens and Gilby, 2004).

Importantly, although evidence obtained from ES is mixed, it is not absent. Seven from 11 tested species showed some evidence for reciprocity and if they were subject to multiple studies, all of them showed reciprocity repeatedly. Eleven different tasks resulted in evidence for reciprocity, ranging from artificial computer tasks (Parrish et al., 2015) to naturalistic field experiments (Seyfarth and Cheney, 1984). This suggests that positive findings are not confined to particular tasks that might be explained by alternative mechanisms. Furthermore, evidence has been demonstrated in 14 independent primate populations from laboratories, sanctuaries, zoos and the wild (Table 1), indicating that reciprocity is neither confined to certain environments nor populations. Finally, evidence for reciprocity in non-human primates has been found in 14 research groups (indicated by different lab managers in the author lists), showing that evidence is not limited to single groups. When leaving aside studies, in which test individuals did not demonstrate task understanding by behaving differently towards a partner being absent or present (indicated with an asterisk in Table 1), there are more tests showing evidence for than against reciprocity

(> 75%, Fig. 1). This demonstration of reciprocity in various contexts suggests reciprocity to be present at least in some primates and under some circumstances; a result that has not been acknowledged but rather ignored.

5. Factors that influence reciprocal cooperation in primates

OS and ES provide overall enough evidence for reciprocity to deserve a closer analysis. The conflicting results, rather than being an indication of no evidence for reciprocity, might be a great opportunity to develop a more integrated and coherent theory. Since studies differ in various aspects from each other, they afford the exploration of the parameter space of the theory of reciprocity. In order to understand under which circumstances reciprocity is exhibited, we will now discuss possible theoretical and methodological reasons for the mixed findings. In addition, we will propose future studies to explore these possibilities in more detail. This may in turn allow us to predict the conditions under which reciprocity emerges and how it is maintained.

5.1. Kinship

Published evidence for reciprocity has been frequently criticised because selective helping might be better explained by kin selection than reciprocal cooperation and thus the latter being only of minor importance (Clutton-Brock, 2009; Stevens et al., 2005). On the one hand, this hypothesis is based on the fact that most cooperative interactions occur among kin, which is true also for primates (Langergraber, 2012). On the other hand, it is based on the general notion that nepotism is a better predictor of cooperation than reciprocity in most non-human animals (Cheney, 2011; Clutton-Brock, 2009; Marshall and Rowe, 2003; Melis and Semmann, 2010). Accordingly, reciprocity has been mainly discussed for non-kin interactions (e.g. Clutton-Brock, 2009). This is reflected in the current literature. Less than 10% of OS have used non-kin only, probably because most cooperation takes place between kin. In contrast, more than 80% of ES have used non-kin to investigate reciprocity.

However, there is no reason to assume that reciprocity does not take place between relatives. In fact, both kin and non-kin show evidence for reciprocity and the results seem not to differ between them (Fig. 2). Especially if interacting with several related individuals, reciprocity might become an important factor to choose the best cooperation partner among multiple relatives. This is consistent with meta-analyses

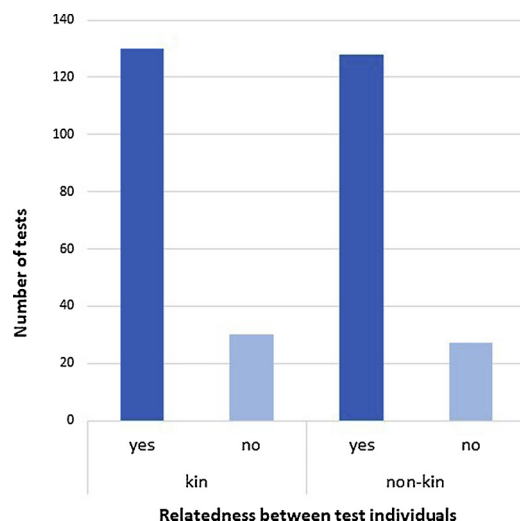


Fig. 2. Dyad relatedness.

Studies on both related and unrelated individuals report more positive than negative findings. There was no difference between related and unrelated dyads.

that found that reciprocity explained food sharing (Jaeggi and Gurven, 2013a) and allogrooming (Schino and Aureli, 2010b) between both kin and non-kin. Moreover, the latter analysis found that reciprocity was even more powerful than nepotism in explaining overall allogrooming levels, suggesting reciprocity to be sometimes more important than nepotism (Schino and Aureli, 2010b).

Furthermore, relatives are not always expected to be preferred as cooperation partners. First, kin commonly live in close proximity, leading to competition over the same resources (Frommen et al., 2007; West et al., 2002). Such competition can sometimes completely level out benefits derived from nepotism (Griffin and West, 2002; Queller, 1994). Under this condition, help should be directed to everybody who has been helpful before, independently of relatedness. In support of this idea, capuchin monkeys are as likely to help kin and non-kin in a token-exchange task (de Waal et al., 2008). Second, kin might not always be the best cooperation partner (Chapais, 2006). Whereas some services, like allogrooming, can be provided by almost all individuals, other services are more difficult to offer because they may depend on age or hierarchy as, for instance, help in agonistic interactions. Therefore, it might be better to form bonds with non-kin, if they can offer additional or different help than kin. Indeed, a long-term field study on chimpanzees concluded that the majority of affiliative dyads were unrelated to each other (e.g. Langergraber et al., 2007). In addition, extending a network to non-kin could be a strategy to decrease the risk of losing primary cooperation partners, as shown in common vampire bats (*Desmodus rotundus*, Carter et al., 2017).

Finally, it has been argued that patterns that look like reciprocity in OS could be the results of increased interactions between kin. Increased time spent in proximity may eventually translate into enhanced opportunities to help, potentially causing a spurious correlation of helpful behaviours (de Waal and Luttrell, 1988). Although symmetrical traits, such as kinship or proximity, can lead to correlations of help as shown in mathematical models (Hemelrijk and Puga-Gonzalez, 2012), this strategy is unlikely to evolve because cheaters may exploit this situation (Campenni and Schino, 2016). For example, if an individual bases its decision to help on proximity, cheaters can easily exploit such individuals by simply staying close to them. Thus, cheaters would benefit from being helped but never invest in helping others. In an evolutionary timeframe, cheaters are expected to reproduce better due to received benefits, which will lead to a slow replacement of cooperators by cheaters within a population. Eventually, the population will consist of cheaters only. Therefore, the possibility of symmetry-based reciprocity is unlikely to explain results from OS. This is consistent with most ES providing evidence for reciprocity that typically control for symmetrical traits, such as proximity or rank (Table 1).

To elucidate the interplay of reciprocity and kin selection, and thus the importance of reciprocity among relatives, it is necessary to manipulate the donation rates of partners that differ in relatedness, preferably without any prior experience to rule out differential bonding states as a confounding effect (cf. Schweinfurth and Taborsky, 2018). This has, however, not been done in primates thus far. In contrast, most ES investigating reciprocity have been conducted on unrelated dyads to rule out that helping decisions might be based on kinship rather than on reciprocity (see also Schino and Aureli, 2010a & Table 1). Only seven tests have been conducted on related pairs. Here five tests found evidence for reciprocity. One study found no evidence for reciprocity and the other was inconclusive because subjects did not pass the task-understanding control (Table 1). Given this small sample size, it is hard to estimate the influence of kinship on reciprocity. Importantly, however, kin selection and reciprocal cooperation are not mutually exclusive and kin-biased help is unlikely to exclusively explain the results of OS.

5.2. Relationship quality

It is conceivable that reciprocity is only exhibited by some dyads and not by others and hence studies may seem to provide conflicting

results depending on the choice of dyads. For example, whether humans show immediate reciprocation is dependent on their relationship. While short-term reciprocity in a tit-for-tat like manner is most common between unfamiliar strangers or business partners, this is generally not the case between close friends that exhibit reciprocity over a longer time scale (reviewed in: Massen et al., 2010; Silk, 2003). In fact, humans prefer to stay in contact with friends that invest in long-term reciprocity (Walker, 1995). If reciprocity were dependent on relationship quality, the choice of dyads is likely to influence the outcome and might explain why some studies find evidence while others do not.

Similar to humans, many primates form differential relationships with group members, including social bonds that may be called friendships (reviewed in: Silk, 2002b). Friends help each other repeatedly and are characterised by equitable and hence reciprocal relationships (Silk, 2003). If primates show relationship-dependent reciprocity comparable with humans, we would predict the following outcomes. In a study focussing on closely bonded individuals, no immediate reciprocation would be expected. In contrast, if loosely bonded, but equally familiar, individuals were chosen, immediate reciprocation could be detected more easily in both ES and OS. In order to test this hypothesis, studies are needed that manipulate the donation rates of partners that are either closely or loosely bonded.

Although this crucial test has not been conducted as far as we know, there is some evidence for the effect of social bonds on reciprocity. Wild chimpanzees share food more often with closely bonded partners with which they shared a reciprocal relationship (Samuni et al., 2018). Importantly, short-term reciprocity cannot explain these findings, as bonding status was a better predictor than prior help. This suggests that no-short-term reciprocity is exhibited between closely bonded chimpanzees. In contrast, chimpanzees were more likely to engage with socially bonded partners in a mutualistic task (Engelmann and Herrmann, 2016) that allowed short-term reciprocity (Engelmann et al., 2015). Similarly, chimpanzees that were less likely to share food in their enclosure (and thus were not closely bonded), were less likely to engage in a mutually rewarding loose-string task (Melis et al., 2006b). However in another task, chimpanzees were equally likely to cooperate with loosely and closely bonded individuals, and adopted a reciprocal strategy with both partners (Calcutt et al., 2019). While these studies demonstrate the influence of social bonding on some helping decisions, it is not yet clear how differential bonding affects reciprocity.

It has been suggested that primates do not keep track of previous help precisely but rather help preferably those with which they associate positive emotions, which is somehow similar to friends, and refuse to help those associated with negative emotions (Schino and Aureli, 2009). In this case, no immediate reciprocation is expected between closely bonded or loosely bonded partners. This hypothesis has not been tested sufficiently. On the one hand, capuchin monkeys direct more help to socially bonded partners than to loosely bonded partners, independently of recently received help (Sabbatini et al., 2012). On the other hand, this study stands in contrast to a study showing that although capuchin monkeys are slightly more prosocial towards in-group members in a token-exchange task, they reciprocate help at equal levels with in- and out-group members, while they had no social bonds with the latter (Suchak and de Waal, 2012). This shows that emotion-based reciprocity is unlikely to explain all decisions to help as help is not exclusively directed at socially bonded individuals (e.g. Goodall, 1986). Given that emotion-based reciprocity has not received much attention yet, further potentially similar studies in a variety of species are needed to understand under which conditions this mechanism is likely to be applied. Another important question is how reciprocal cooperation influences the likelihood of bonding with partners.

5.3. Partner choice

Reciprocity always involves a time delay between received and given help, which is why it is vulnerable to cheating, i.e. free-riding by

not paying back already received help, and which is why there has been considerable scepticism about the explanatory power of reciprocity. It has been assumed that to overcome the potential risk of cheating, mechanisms of cheater detection have evolved. Two different mechanisms have been proposed to detect and avoid cheaters. On the one hand, individuals may avoid cheaters and selectively approach co-operators in the future, i.e. partner choice (Noë and Hammerstein, 1995). On the other hand, individuals may control the cheater's future behaviour by withdrawing from helping or by actively punishing them, i.e. partner control (Trivers, 1971). If one mechanism is more likely to explain reciprocity in non-human primates than the other, studies can result in mixed findings.

There is good evidence that humans control their partner's behaviour by not only withdrawing help from cheaters but also by punishing them. Indeed, humans are even willing to incur monetary costs to punish cheaters (Fehr and Gächter, 2002). Although punishment is apparently rare in other animals (Riehl and Frederickson, 2016), there is some evidence for non-human primates (Raihani et al., 2012). In non-reciprocal contexts, chimpanzees punish cheaters, which had stolen food from them (Jensen et al., 2007) but not if cheaters had stolen from others (Riedl et al., 2012). In addition, chimpanzees were shown to protest, displace and punish free-riders in a mutually rewarding loose-string task, suggesting the operation of some partner control mechanisms (Suchak et al., 2016). However, the results stand in contrast to natural observations, for instance on border patrols in chimpanzees. Such patrols are costly not only in terms of time and energy but can also prove lethal. Thus, one would expect reciprocity to occur. Surprisingly not all males engage in this behaviour equally often and no punishment has been recorded for not participating (Mitani, 2009). Given these few studies, future research is needed on a range of species to test for the prevalence of partner control mechanisms in primates, for instance by investigating their behaviour towards conspecifics that were made to be cheaters or happen to be cheaters naturally.

Unlike partner control, individuals can choose to help cooperators by simply avoiding cheaters. Such partner choice can lead to reciprocal cooperation and is assumed to be widespread among primates (Schino and Aureli, 2017). Partner choice based on experienced help is difficult to observe in OS as it is often invisible. Therefore, ES are needed. Few studies (9 of 31) allowed individuals to choose their cooperation partners. Importantly, all of these tests provided evidence for reciprocity (Table 1). As far as we are aware, only one test has experimentally directly compared the predictive power of partner control over choice and found that capuchin monkeys showed partner choice in trios and partner control in duos, whereas the latter effect was weaker (Sabbatini et al., 2012). This result is consistent with a recent review that concluded that partner choice may explain reciprocity in non-human primates better than partner control (Schino and Aureli, 2017).

In addition, reciprocity might be a result of both mechanisms, which may explain the evidence for partner control and choice in the same species (Table 1). For instance, capuchin monkeys seem to use both partner control (e.g. de Waal, 1997a) and partner choice (Sabbatini et al., 2012). In addition, chimpanzees in a bar-pulling task showed partner choice and partner control (Suchak et al., 2016). Future studies are needed to disentangle these two mechanisms, for instance, by giving test subjects the choice of both partner control and choice. Although partner choice is hard to test under natural conditions, mainly because not choosing a partner is usually not visible, behavioural observations of individuals not responding to requests might indicate partner choice in the wild.

5.4. Temporal aspects

Most studies differ in an important aspect; the time period in which interactions take place, which has a major effect on the cognitive mechanisms required for reciprocity. The delay between received and given help can take seconds to weeks (see below) with very different

consequences and constraints. While reciprocating over short time scales might be easier to memorise, it might not be feasible for some behaviours under natural conditions. For instance, support in fights can rarely be immediately reciprocated. In addition, short-term reciprocity may imply immediate turn-taking, which is rather inflexible. At the end of the temporal spectrum, long time delays result in increased memory errors, especially when interacting with multiple partners (Stevens et al., 2011).

Some ES require test subjects to take turns immediately after having received help once (see below). The prediction to find immediate turn taking such as “one for you and one for me”, is probably based on theoretical work. In fact, tit-for-tat is a way to describe immediate turn taking and it has been shown to be a powerful theoretical strategy against cheaters (e.g. Axelrod and Hamilton, 1981). However, such immediate strategies are relatively inflexible as cooperation breaks down quickly after an individual fails to help once (Zagorsky et al., 2013). In addition, almost all natural forms of cooperation are not an all-or-nothing response, which theoretical models assume, but rather a continuous variable, e.g. allogrooming more or less, which is why immediate turn-taking is probably of minor importance. Hence, many other strategies are available that enable reciprocity without turn taking (e.g. Gurven, 2006). Furthermore, turn taking might be cognitively more challenging than increasing help after receiving help multiple times. For example, chimpanzees did not take turns between the roles of donor and recipient in a food donation task, although the same individuals reciprocated help in a more free condition (Yamamoto and Tanaka, 2009). Turn-taking seems to be cognitively demanding for humans, too, exemplified by children who start taking turns at around the age of five (Melis et al., 2016), which is two years after they can reciprocate help (Warneken and Tomasello, 2013). The authors highlight that turn-taking is commonly assisted by explicit communication, e.g. “Let’s always take turns”, which chimpanzees apparently lack and may explain why they failed in this task (Melis et al., 2016).

In contrast to turn taking, there is evidence for short-term reciprocity in primates. For instance, allogrooming has been shown to be reciprocated within a single interaction bout in blue monkeys, *Cercopithecus mitis* (Cords, 2002), bonnet macaques, *Macaca radiata* (Manson et al., 2004), chacma baboons, *Papio cynocephalus ursinus* (Barrett et al., 1999), crested macaques, *Macaca nigra* (Dunayer et al., 2019), rhesus macaques, *Macaca mulatta* (Dunayer et al., 2019), sooty mangabey, *Cercocebus atys* (Fruteau et al., 2011), vervet monkeys (Fruteau et al., 2011) and white-faced capuchins, *Cebus capucinus* (Manson et al., 2004). Further, help has been shown to be reciprocated within slightly longer time frames, i.e. minutes. For instance, mandrills (*Mandrillus sphinx*) and capuchin monkeys showed a higher probability to groom partners that groomed them immediately before (Schino et al., 2009; Schino and Pellegrini, 2009). In addition, bonobos, unlike chimpanzees, showed short-term reciprocity when exchanging food with allogrooming (Jaeggi et al., 2013).

These studies show that many primates might be capable of reciprocating favours over short time frames. However, exchanging grooming for support in Japanese macaques (*Macaca fuscata*) was better explained by long-term than short-term timeframes (Schino et al., 2007). Furthermore, a meta-analysis concluded that only between 7% and 35% of all allogrooming bouts are reciprocated over short time periods in non-human primates (Schino and Aureli, 2017). The remaining allogrooming was better explained over long-term timeframes and shows that reciprocity can take place more often over large time scales, potentially over several weeks.

Thus, non-human primates show evidence of reciprocity over short and long timeframes. Still, future studies are needed to investigate under which conditions short over long timeframes are preferred and which timeframes are relevant for a given species and why (cf. Schino and Pellegrini, 2009). Furthermore, we need to explore how and what information individuals memorise about their partners in order to understand how memory may constrain the time scale of reciprocity. This

includes, for instance, how much information needs to be stored, how specific does the information need to be and how many partners can be memorised.

5.5. Experimental design

Over 80% of studies investigating reciprocity in non-human primates are observational. Such studies have been frequently criticised for potential alternative explanations (e.g. Cheney, 2011; Seyfarth and Cheney, 1988). Hence, experimental manipulations are important additions to OS when trying to disentangle conditional from unconditional help in order to demonstrate reciprocity. Thereby it is important to ensure test validity (see also: Hauser et al., 2009; McAuliffe and Thornton, 2015). However, designing a good experimental test is not trivial and needs sometimes rather complex setups. For this, it is crucial that every test subject is motivated to participate and understands the task. A lack of both may result in negative results, which does not reflect the test animals’ inability to reciprocate but rather their inability or reluctance to use an apparatus.

Designing a meaningful task for another species can be challenging and there is no straightforward solution. First, it is important to ensure that test subjects are motivated to participate and pay attention (Brosnan, 2017) because a lack of motivation may result in low helping rates independently of what the partner has done before. Additionally, even if we think a task is intuitive, it may not be so for another species. Therefore, task-understanding controls, tailored to each test, are necessary. A recent review concluded that almost 75% of prosocial choice studies on primates have not tested for task understanding (Marshall-Pescini et al., 2016). Although ES investigating reciprocity in non-human primates have conducted more such controls, still over 35% have not reported a task-understanding control or referred to an earlier study using the same task (indicated in Table 1). In addition, seven tests reported results for individuals that have not shown a different response towards an empty cage, indicating a potential lack of motivation or understanding as noted also by the authors (Amici et al., 2014; Pelé et al., 2009). All studies, in which test subjects did not demonstrate task understanding, did not show evidence for reciprocity.

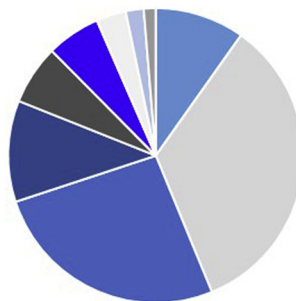
Thus, the results of more than half of the available evidence obtained in ES are difficult to interpret (19 of 31 tests). One possibility to ensure task comprehension is to give subjects enough access to the task before the test. However, this can lead to overtraining and thus an overestimation of given help (Marshall-Pescini et al., 2016). Another possibility is to try to mirror natural contexts, as has been done for instance by manipulating natural behaviours (Hemelrijk, 1994) or using playbacks (Seyfarth and Cheney, 1984).

5.6. Commodity characteristics

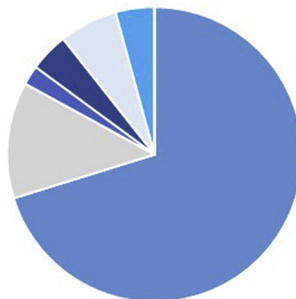
Studies differ vastly in the choice of commodity, which can potentially impact the use of reciprocal strategies. We have identified at least eleven different types (Table 1, tab. S1, Fig. 3). Importantly, studies that investigated food produced less evidence for reciprocity than studies involving non-food related commodities, like allogrooming or support. In particular, studies involving food resulted only in 61% in OS and 60% in ES in evidence for reciprocity. However, studies involving other commodities resulted in 82% in OS and 100% in ES in evidence for reciprocity. This illustrates that the choice of commodity impacts the results. Especially, food sharing is a particular form of help, which is less likely to be exchanged for at least two reasons.

First, food sharing is, as far as we are aware, the only commodity where individuals need to give away already possessed material and thus donors immediately lose something. This stands in contrast to other services like allogrooming, consolation, copulation or support, which are provided without relinquishing a prior possession. Therefore, food sharing is likely to be reduced or constrained by loss aversion (Kahneman and Tversky, 1984). Capuchin monkeys, for instance, avoid

a) observational studies



b) experimental studies



commodity	OS	ES
food	10%	70%
allogrooming	34%	13%
support	26%	2%
tolerance	11%	4%
aggression	7%	0%
assistance	0%	6%
mating	6%	0%
attention	0%	4%
infant handling	3%	0%
play	2%	0%
affiliative	1%	0%

Fig. 3. Commodities of reciprocal exchanges.

Non-human primates have been shown to exchange at least eleven different types of commodities. These are: food sharing (i.e. providing food items to conspecifics), allogrooming (i.e. gentle cleaning a conspecific's fur), supporting (i.e. attacking one individual that was in an agonistic interaction with another), aggression (i.e. displaying, threatening or fighting a conspecific), assisting (i.e. opening a door for a conspecific), mating (i.e. copulating with a sexually mature individual of the opposite sex), attending (i.e. looking at or approaching a conspecific or a loud speaker playing back its call), infant handling (i.e. touching, holding, allogrooming, nursing and carrying an infant of another conspecific), playing (i.e. nonviolent attacking and fighting a (juvenile) conspecific), and affiliative behaviours (i.e. category composed of several prosocial behaviours including touching, vocalising, contact sitting, huddling). While ES focus mostly on food donations (panel a), the pattern is more diverse in OS (panel b), with support and allogrooming being the most commonly investigated commodities.

losing coins that can be traded for food, even if the outcome would be the same by giving away some coins (Chen et al., 2006). This example shows that loss aversion does not make sharing impossible as capuchins have been repeatedly shown to share food reciprocally (Table 1). It may explain, however, why sharing is mostly passive and at low levels in this species (de Waal, 2000, 1997a). Furthermore, many primates show respect for possession, which could additionally lower the motivation to share food because potential recipients may not expect or request sharing (Brosnan, 2011).

Second, whereby many ES involve food, food sharing is not overly common among wild primates, which is reflected by OS mostly investigating support and allogrooming (Fig. 3). Only 50% of primate species show food sharing between parents and their offspring, while sharing among adults has been reported in less than 20 species (Jaeggi and Gurven, 2013b). Even in these species, the food is seldom actively shared, but food is rather passively shared by tolerating thefts. The limited need to share food under natural conditions is probably explained by the omnivorous diet of most primates and the generally scattered distribution of food (Jaeggi and Gurven, 2013b). Instead of sharing, many primates are competitive over food (Janson and van Schaik, 1988). An interesting exception are Callitrichids, which include marmosets and tamarins, which are the only non-human primates that systematically share food proactively (Jaeggi et al., 2010). Yet, it is unclear whether their high motivation to share food interacts with their

ability to reciprocate. While common marmosets (*Callithrix jacchus*) readily share food with each other at high levels even when reciprocity is excluded in the study design (Burkart et al., 2007), the closely related cotton-top tamarins share more food with others, if there is the possibility to reciprocate favours (Cronin et al., 2010; Hauser et al., 2003).

Based on these two aspects, food differs in important aspects from other commodities that non-human primates use to help each other. Currently there are only few ES available, investigating reciprocity of non-food help. Notably, all of them have resulted in evidence for reciprocity (Table 1). Future studies are needed to understand which characteristics of different commodities impact the likelihood of them being reciprocated. For this, additional paradigms need to be developed that investigate the reciprocity of other commodities than food. A good candidate would be allogrooming that is probably the most common affiliative behaviour in primates (Schino and Aureli, 2008). In order to manipulate this behaviour, substances may be applied on individuals (Hemelrijk, 1994; Schweinfurth et al., 2017). Another important test would be to directly compare different commodities in the context of reciprocity, for instance, by providing test subjects with the choice of providing one or another service.

Still, the use of food in ES has many benefits, such as increasing the subject's motivation to participate or the easy and quantifiable manipulation and measurement of help. Given the obvious assets of using food, some researchers came up with elaborate ideas to design a food-motivated task without involving food in the first place, i.e. exchanging food with inedible tokens (Brosnan and de Waal, 2003) or wrapping food to make it invisible (Horner et al., 2011). Whether this resembles general commodity exchanges needs to be validated, however.

6. Conclusions

Since Trivers (1971) proposed reciprocity as one mechanism that could enable cooperation, it has been tested multiple times in various species, including non-human primates. Indeed, primates appear to be great study candidates as they fulfil all social and cognitive prerequisites for reciprocity to occur. Until now, more than 150 articles have been published in peer-reviewed scientific journals on this topic. Based on this literature, it is still widely believed that reciprocity is of minor importance in primates (e.g. Clements and Stephens, 1995; Clutton-Brock, 2009; Hammerstein, 2003; McAuliffe and Thornton, 2015; Ramseier et al., 2006; Stevens et al., 2005; Stevens and Gilby, 2004). Scepticism is based on mixed and negative findings. In this review, we challenged this belief.

First, we reviewed the literature and found that there are in fact more positive than negative findings. Evidence in favour of reciprocity stems from OS and ES, which used various study designs and species. This shows that contrary to current perception, reciprocity might be a common mechanism of cooperation in non-human primates. Furthermore, reciprocity might have been even underestimated in OS because reciprocity can be masked by help between relatives and trading between commodities. In addition, we found that most negative findings obtained in ES come from studies, in which either task understanding was not tested, or the test subjects failed to show such understanding, leading possibly to an overestimation of negative findings. In summary, the evidence is neither rare nor absent, and when mixed there are likely explanations. Consequently, the potential of reciprocity in the evolution of primate cooperation needs to be revisited.

Second, while most studies find evidence for reciprocity, some do not. Although such studies have been interpreted as a failure to prove the theory of reciprocity, we think that such findings give valuable insights into the mechanisms of reciprocity because they can explain under which circumstances reciprocity is most likely to be expressed. For instance, we show that reciprocity is not confined to unrelated individuals, but the relationship quality might impact the likelihood to reciprocate. In addition, choosing partners, rather than controlling them, can explain variability in the results. The temporal setting of

paying back received help varies between species and there is evidence for both short and long-term reciprocity but not for immediate turn taking. Finally, the choice of commodities can impact the results, such as food donations seem to be a peculiar kind of help that is less likely to be reciprocated.

Throughout the article, we pointed out experiments that can help us understand the parameter space of the theory of reciprocity. To estimate the influence of kinship on reciprocity, donation rates of partners that differ in relatedness need to be manipulated. Likewise, to estimate the influence of relationship quality, donation rates of loosely and closely bonded partners need to be manipulated. Further, to understand whether reciprocity is explained by partner control or partner choice mechanisms, both mechanisms must be directly compared. Different timeframes and their impact on reciprocity need to be studied both empirically and theoretically. Finally, by providing test individuals with the choice between several commodities, we will be able to investigate the impact of different commodities on reciprocity. These future studies will help us to understand more about its occurrence, proximate and ultimate mechanisms, which will in turn inform us about the evolutionary origins of reciprocity. The debate about reciprocity in non-human primates is by no means limited to our closest living relatives (e.g., Carter, 2014; Taborsky, 2013). Results on a variety of species will unravel general patterns in the evolutionary pathways. Perhaps most strikingly is that although humans have been termed “*Homo reciprocans*”, surprising little is known about the psychological mechanisms of our own reciprocity.

In conclusion, our review shows that reciprocity is more common and probably more important than currently believed. The present evidence should not be disregarded, and negative findings not used as evidence of no reciprocity but as the building blocks for a more comprehensive theory. To progress, we should rather aim at understanding when and how reciprocity is shown in non-human animals than asking whether it is present.

Acknowledgments

We would like to thank Joachim Frommen for helpful discussions and comments and four anonymous referees for their insightful and constructive feedback. The Swiss National Science Foundation provided funding to MKS (grant number P2BEP3 175269). The European Research Council provided funding to JC (Synergy grant 609819 SOMICS).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2019.06.026>.

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- was shaped by natural selection because it provides benefit to others (Sachs et al., 2004; West et al., 2007).
- Helping:** A behaviour by which one individual benefits one or several other partners (Taborsky et al., 2016; West et al., 2007).
- Reciprocity:** Individuals exchanging goods and services that are contingent on each other (Trivers, 1971).
- Reciprocity: Proximate causation:** The behavioural, psychological (including cognitive, motivational, emotional), endocrinological and neurophysiological processes that enable individuals to show reciprocity. The combination of different processes give rise to different reciprocity mechanisms. Four main mechanisms have been described in the literature: 1) Hard-wired reciprocity: Individuals respond automatically to received help by immediately returning it. 2) Attitudinal reciprocity: Individuals help others based on an attitude that was formed during the most recent cooperation event with this partner. 3) Emotional reciprocity: Individuals help preferably partners with which they associate positive emotions, which are the result of repeatedly cooperating with each other. 4) Calculated reciprocity: Individuals base their decision to reciprocate help on a track record of the amount and value of received help by a partner (Brosnan and de Waal, 2002; Schino and Aureli, 2009).
- Reciprocity: Ultimate causation:** The fitness payoff structure that causes natural selection to favour the evolution of reciprocity. Reciprocity can only evolve if individuals exchanging help reciprocally will receive a better net fitness payoff than individuals that do not reciprocate. Three main strategies have been described in the literature: 1) Generalised reciprocity: An individual receives help by a partner. Based on this experience, the individual will help someone, independently of its identity. 2) Direct reciprocity: A partner helps an individual, who will help the partner in return. 3) Indirect reciprocity: A partner helps someone, and this act is witnessed by a third individual. Therefore, this individual is more likely to help the cooperative partner (Axelrod and Hamilton, 1981; Nowak, 2006).

Glossary

Cooperation: An act by one individual that benefits one or several other partners. The act